Extractrix dockeryi, a new species from the Eocene of the southeastern United States, with notes on open coiling in the Cancellariidae (Gastropoda: Neogastropoda)

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ABSTRACT

Extractrix dockeryi is described from beds of Middle Eocene (Bartonian) age in the Gosport Sand Formation at Little Stave Creek, Alabama and the contemporaneous McBean Formation at Orangeburg, South Carolina. This new species represents the earliest occurrence of open coiling in the family Cancellariidae. Other records of open coiling in the Cancellariidae are reviewed, and the taxonomic status and composition of the genus *Extractrix* is discussed.

Additional Keywords: Cancellariidae, *Extractrix*, open coiling, Eocene

INTRODUCTION

We report the discovery of a new species of open-coiled cancellariid from two different Middle Eocene (Bartonian) deposits in the southeastern United States, one, the Gosport Sand Formation at Little Stave Creek, Alabama, the other, the McBean Formation at Orangeburg, South Carolina. This new species represents the earliest known occurrence of open coiling in the family Cancellariidae. It is assigned to the genus *Extractrix* Korobkov, 1955, based on similarities to its type species, *Extractrix extractrix* (Boettger, 1906), from Middle Miocene (Badenian) deposits of the Transylvanian Basin in Romania (Lăpugiu de Sus). We review the literature for other records of whorl detachment in the Cancellariidae, and discuss the taxonomic status and composition of the genus *Extractrix*.

OCCURRENCE OF OPEN COILING IN CANCELLARIIDAE

Whorl detachment, the lack of contact between successive whorls of a coiled shell, is rare among gastropods. The degree and regularity of whorl detachment may vary considerably, from simple detachment of portions of the final whorl, as in *Valvata sincera ontariensis* Baker, 1931 (see Clarke, 1973: 225, pl. 20, figs. 8,9) to the occurrence of multiple detached and loosely or irregularly coiled whorls, as in *Tenagodus squamatus* (Blainville, 1827) (see Abbott and Dance, 1982: 61, as *Siliquaria squamata*). We follow Yochelson, (1971: 236) in applying the term "disjunct" to forms that have a detached last whorl; "uncoiled" to forms in which coiling is very irregular; and "open-coiled" to forms in which the whorls are detached, yet coiling conforms closely to a logarithmic spiral.

The prevalence of whorl detachment within particular gastropod taxa may also vary. Disjunct, uncoiled and open-coiled forms of whorl detachment may occur as unique or rare events in normally coiled species, either as teratalogical or gerontic (Yochelson, 1971: 236) conditions, or as a malformation following unsuccessful predation involving shell breakage. Whorl detachment may also occur more widely in predominantly tightly coiled taxa [e.g., in *Spirolaxis rotulacatherinea* (Melvill and Standen, 1903), see Bieler, 1993:325, figs. 268-270; or in *Valvata juliae* Scholz and Glaubrecht, 2010, (their fig. 2 documents frequencies of open coiling of up to 25% in various populations)]. Detached whorls may also become a fixed character of a species or subspecies. Rex and Boss (1976) reviewed the incidence of such open-coiling in Recent gastropods and reported that it occurs at very low frequency ($\approx 7.5\times10^{-4}$). Among the examples they documented, 26.7% were planispiral species in which open coiling was due primarily to increases in the distance of successive whorls from the axis of coiling [high values of D, according to the terminology of Raup's (1961, 1966) model of shell coiling]. For the majority of taxa (60.0%), open coiling was a consequence of elongation of the shell along the axis of coiling [high whorl translation rate, T (Raup, 1961; 1966)], while 13.3% of the taxa were open-coiled according to both criteria. In some instances, open coiling appears to be sufficiently adaptive to have given rise to diversified open-coiled lineages [e.g., *Cycloscala* Dall, 1889 (Epitoniidae); *Eccliseogyra* Dall, 1892 (Nystiellidae) ; *Extractrix* Korobkov, 1955 (Cancellariidae)].

Known instances of whorl detachment within the family Cancellariidae are listed in Table 1. *Extractrix extractrix*, *E. dockeryi* new species, and *E.milleri* (Burch, 1949) all show a marked increase in the degree of elongation (increase in the whorl translation rate, T) at the protoconch / teleoconch transition, resulting in open coiling for all teleoconch whorls (only the first 0–½ teleoconch whorls are in contact with prior whorls). Although Janssen (1984a: 21) considered *Trigonostoma protrigonostoma* Sacco, 1894 to be closely related to *Extractrix extractrix*, the former has a shell (Sacco, 1894: pl. 1, figs. 3a,3b) that more closely resembles *Trigonostoma umbilicare* (Brocchi, 1814), differing from that species in having a portion of the body whorl (~ ½ whorl) disjunct. In contrast, the early teleoconch whorls of *Trigonostoma* ("*Extractrix*") *hoerlei* Olsson, 1967 are nearly planispiral, with the increase in the elongation rate occurring in the second teleoconch whorl (Figure 23, arrow), resulting in a shell in which only the last 1–1½ whorls are disjunct. There is a report (Coucom, 1975) of a single disjunct specimen of *Trigonostoma scalare*, a species that is normally coiled, in which the last ½ whorl is detached.

SYSTEMATICS

Family Cancellariidae Forbes and Hanley, 1851
Subfamily Cancellariinae Forbes and Hanley, 1851

Genus *Extractrix* Korobkov, 1955

Pseudomalaxis (*Extractrix*) Korobkov, 1955:138. Type species: *Pseudomalaxis extractrix* (Boettger, 1906) by original designation.
Trigonostoma (*Extractrix*) Olsson, 1967:23-24.

Diagnosis: Shell small to medium-sized (to 27 mm), with tall, conispiral, deeply umbilicate, open-coiled shell. Protoconch of smooth, evenly rounded whorls. Transition to teleoconch marked by major increase in degree of elongation along the axis of shell coiling, resulting in loss of contact between whorls within first ½ teleoconch whorl. Teleoconch of up to 4 whorls, sharply triangular in cross-section. Carinae along shoulder and siphonal canal with open spines (long to barely discernible).

Remarks: The type species of *Extractrix* was described as *Discohelix* (*Pseudomalaxis*) *extractrix*, in the family Architectonicidae by Boettger (1906: 138), and retained in this family by subsequent authors (e.g., Cossmann, 1916; Zilch, 1934), including Korobkov (1955), who proposed *Extractrix* as a subgenus of *Pseudomalaxis*. Citing Boettger's (1906: 138) reference to two small columellar plaits, Olsson (1967:23) transferred *Extractrix* to the family Cancellariidae, as a subgenus of *Trigonostoma*, but regarded it as a "form genus" and questioned the relationship of its type species to other loosely coiled cancellariids. Janssen (1984a: 20) treated the type species as belonging to *Trigonostoma sensu stricto*, and considered it to be closely related to *Trigonostoma protrigonostoma* Sacco, 1894, a species in which only a portion of the body whorl is disjunct. Harzhauser and Landau (2012: 56) regarded the status of the genus *Extractrix* as questionable. They considered the species assigned to this genus to form a morphological group based on open coiling that was not necessarily monophyletic, but possibly an assemblage of independently evolved, uncoiled species of *Trigonostoma*.

Prior authors have assigned cancellariid species to the genus *Extractrix* primarily, if not exclusively on the basis of the presence of either disjunct whorls or open coiling, an approach that has rendered this genus paraphyletic. The updated diagnosis of *Extractrix* is based on more precisely defined shell characters that are shared by the type species and some, but not all cancellariid species with disjunct or open coiled shells. We conclude that these characters are sufficient to define a clade that is related to *Trigonostoma*, but has persisted from the

Table 1. Records of whorl detachment within the family Cancellariidae.

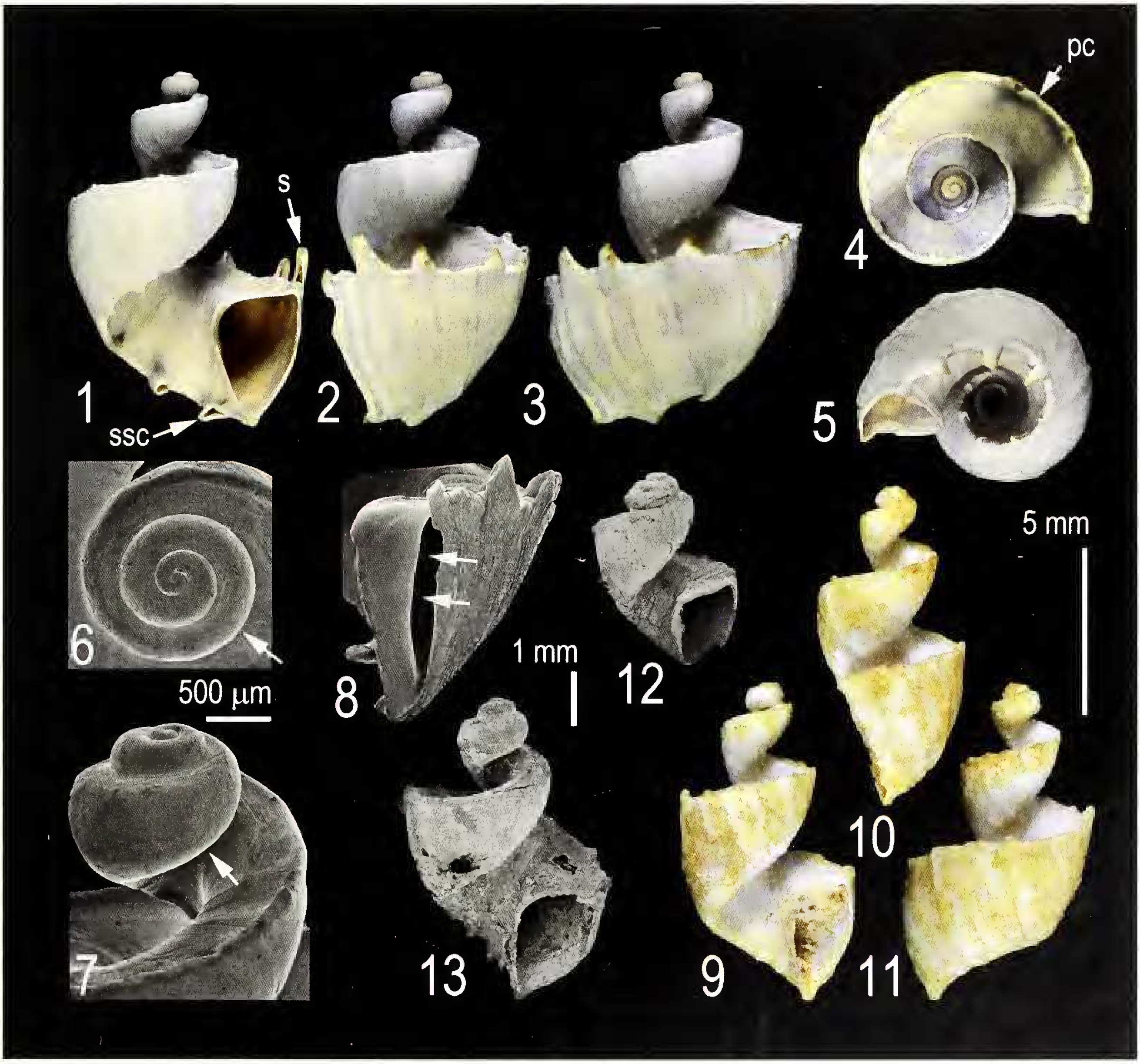
Taxon	Age	Geographic Range	Coiling Type	No. of known specimens[1]
Extractrix dockeryi new species	Eocene	SE USA	Open	4
Extractrix extractrix (Boettger, 1906)	Miocene	S + E Europe	Open	4+?
?*Extractrix* cf. *extractrix* Janssen, 1984a,b[2]	Miocene	N Europe	Open	35
Extractrix milleri (Burch, 1949)	Pleistocene-Recent[3]	E Pacific Galapagos[3]	Open	>50
Trigonostoma protrigonostoma Sacco, 1894	Miocene	Europe	Disjunct (~ last ½ whorl)	1+?
Trigonostoma hoerlei Olsson, 1967	Pliocene	E USA + Caribbean[4]	Disjunct (last whorl)	> 6
Trigonostoma scalare Gmelin, 1791	Recent	Indo-Pacific	Disjunct[5] (~ last ½ whorl)	1

[1] Number of specimens with detached whorls reported in the literature.
[2] Harzhauser and Landau (2012:56) suggested that the specimens from the Netherlands reported by Janssen (1984a,b) represent a species different from *E. extractrix*.
[3] Landau *et al*. (2012:223)
[4] Jung (1977) reported this species from the early Pliocene Punta Gavilán Formation of coastal Venezuela.
[5] Coucom (1975)

Eocene to the Recent, with records in the eastern Pacific [Pleistocene-Recent], southeastern United States [Eocene] and northern and eastern Europe [Miocene].

Extractrix dockeryi **new species**
(Figures 1–13)

Description: Shell (Figures 1–13) small (to 10.7 mm) thin, with tall, narrow (spire angle 51–66°), conispiral, deeply umbilicate, open-coiled shell. Protoconch (Figures 6, 7) increasing in diameter from 83 µm to 1.09 mm in 2¾ smooth, evenly rounded whorls, deviated from teleoconch axis by ~9°. Transition to teleoconch distinct, marked by slight change in surface texture and curvature (Figures 6, 7, arrows), as well as a major increase in the degree of elongation along the coiling axis of the shell [rate of whorl translation, T (Raup, 1966) increasing from ~1.5 for the protoconch to ~3.25 for



Figures 1–13. *Extractrix dockeryi* new species. **1–8.** Holotype, UF 242210, Little Stave Creek, Alabama. **1.** Apertural. **2.** Lateral, **3.** Dorsal, **4.** Apical, and **5.** Umbilical views of the shell. **6.** Apical and **7.** Lateral views of the protoconch. Arrows indicate transition from protoconch to teleoconch. **8.** Columella. Arrows indicate vestiges of columellar folds. **9–11.** Paratype 1, Petit Collection 3488, about 3 miles WNW of Orangeburg, Orangeburg County, South Carolina. **12–13.** Paratypes 2 and 3. FMNH 328571. Edge of Caw Caw Swamp, WNW of Orangeburg, Orangeburg County, South Carolina. 5 mm scale bar applies to Figures 1–5 and 9–11; 500 µm scale bar applies to Figures 6, 7; 1 mm scale bar applies to Figures 8, 12, 13. Abbreviations: **pc**, peripheral carina; s. shoulder spines; **ssc**, siphonal canal spines.

teleoconch] that results in none of the teleoconch whorls being in contact with each other. Teleoconch with up to 2½ sharply shouldered whorls that are strongly triangular in cross section. The adabical portion of each whorl is flat, tabulate, nearly perpendicular to coiling axis (forming an angle of 70–82°), the abaxial margin is demarcated by a sharply angled shoulder with a weak peripheral carina (Figure 4, pc) bearing broad, open spines. Outer portion of each whorl weakly convex, sinuate and recurved at juncture with short siphonal canal. Columellar portion of each whorl straight, nearly parallel to coiling axis in early whorls (Figures 12, 13), angle increasing up to 22° in later whorls (Figure 1). Outer portion of whorl and columella form an acute angle (30–39°), bearing a carina along their juncture, while the juncture of the columella and the adapical region is evenly rounded. Spiral sculpture absent or limited to barely perceptible, extremely fine spiral threads on portions of the outer surface of the last whorl. Axial sculpture of simple, weak, prosocline, growth striae, raised, open spines (Figure 1, s) along shoulder (8–11 on last whorl), and weaker, adaxially deflected open spines (Figure 1, ssc) along the carina at the anterior edge of the siphonal canal (0–7 on last whorl). Spines on shoulder and siphonal canal may be prominent or weak and worn. Aperture triangular, with short, pronounced siphonal canal. Outer lip smooth, columella with two very weak columellar folds (Figure 8, arrows).

Type Material: Holotype, Florida Museum of Natural History, University of Florida, UF 242210; Paratype 1, Petit Collection 3488, About 3 miles WNW of Orangeburg, Orangeburg County, South Carolina, [McBean Formation, Middle Eocene (Bartonian)]; Paratypes 2-3. The Field Museum, FMNH 328571, Edge of Caw Caw Swamp, WNW of Orangeburg, Orangeburg County, South Carolina [McBean Formation, Middle Eocene (Bartonian)].

Type Locality: Little Stave Creek, Clarke County, Alabama [Gosport Sand Formation, Claiborne Group, Middle Eocene (Bartonian)].

Distribution and Habitat: This species is presently known from the type locality as well as from the McBean Formation, WNW of Orangeburg, South Carolina. Both deposits are of Middle Eocene (Bartonian) age. The sand deposits at the type locality were "probably laid down in less than 20 fathoms [36.6 m] of water" (Gardner, 1957: 584). The Orangeburg Sand of the McBean Formation correlates with the Gosport Sand (Dockery et al., 1992) and was also deposited on a shallow marine shelf, mainly in low energy conditions (Nystrom et al., 1991).

Etymology: This new species honors Dr. David T. Dockery III, of the Office of Geology, Mississippi Department of Geology and Environmental Quality, in recognition of his many contributions to the study of the Tertiary paleontology of Alabama and Mississippi.

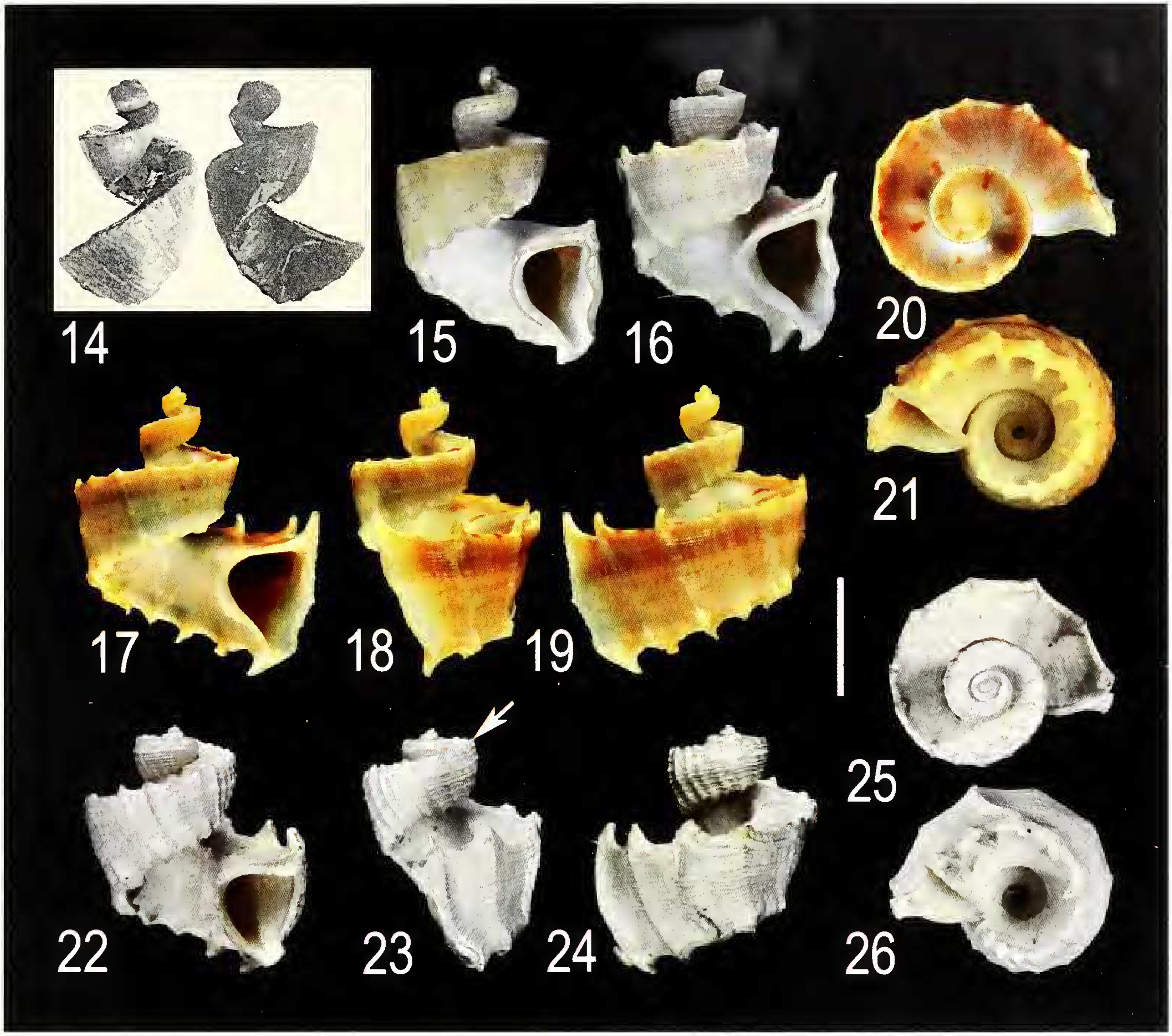
Comparative Remarks: This new species most closely resembles *Extractrix extractrix* (Boettger, 1906), the type species of the genus *Extractrix* Korobkov, 1955 (Figure 14), a Miocene species that has been reported from the Burdigalian-Langhian of Romania (Boettger, 1906) and the Netherlands (Janssen, 1984a,b) as well as from the Messinian of Italy (Davoli, 1995). Both species have open-coiled shells in which teleoconch whorls are not in contact due to high rates of whorl translation ($T = 3.0–3.8$), sharply triangular whorl profiles, and lack pronounced spiral sculptural elements. *Extractrix dockeryi* new species differs from *E. extractrix* in having proportionally broader, more inflated whorls, and pronounced carinae along the shoulder, and at the end of the short, constricted siphonal canal. The presence of open spines distinguishes *E. dockeryi* from Romanian and Italian specimens of *E. extractrix*, but specimens from the Netherlands may have low spines along both carinae that may be connected by weak axial ridges (Janssen, 1984a: pl. 2, fig. 16; 1984b: pl.66, figs. 6,7). Harzhauser and Landau (2012: 56) suggested that the specimens from the Netherlands represent a species different from *E. extractrix*. *Extractrix dockeryi* is easily distinguished from its Pleistocene-Recent congener, *E. milleri* (Burch, 1949) (Figures 15-21), a species from the tropical eastern Pacific that has a much larger (to 26 mm), broader shell with axial and spiral sculpture.

DISCUSSION

As more rigorously defined, the genus *Extractrix* contains its type species *Extractrix extractrix* from the Miocene of Europe, *E. dockeryi* new species from the Eocene of the southeastern United States, and *Extractrix milleri* from the Pleistocene-Recent of the tropical eastern Pacific. In the event that the specimens from the Miocene of the Netherlands that had been attributed to *E. extractrix* by Janssen (1984a, b) are segregated as a separate species, as suggested by Harzhauser and Landau (2012), this too should be included in *Extractrix*. Both "*Trigonostoma*" *hoerlei* and "*Trigonostoma*" *protrigonostoma* are excluded from *Extractrix* as both have disjunct rather than open coiled shells. The relationship of *T. hoerlei* (Figures 22–26) appears closer to some species of *Ventrilia*, suggesting an independent origin of whorl detachment.

The genus *Extractrix* appears to have originated in the western Atlantic during the Eocene and spread eastward to Europe, where widespread populations (North Sea, Paratethys and Tethys Basins) were present during the Miocene. It survives in the Recent fauna as a paciphile genus, which once inhabited the western Tertiary Caribbean Province, but is now presumably extinct there and survives in eastern Pacific waters (Woodring, 1966: 426).

Open coiling is generally regarded as maladaptive as it increases vulnerability to shell breaking predators and impedes mobility, but may survive in situations where such ecological limitations are relaxed (e.g., when



Figures 14–26. *Extractrix* species. **14.** *Extractrix extractrix* (Boettger, 1906). Lectotype, Lăpugiu de Sus, Romania (Specimen lost, see Harzhauser and Landau, 2012: 56. Figures from Cossmann 1916: pl. 12, figs. 25–26). **15–21.** *Extractrix milleri* (Burch, 1949). **15.** Apertural view of Holotype USNM 600660, Near Punta Arenas, Tambor, Costa Rica. **16.** Apertural view of USNM 679301, Guaymas, Mexico. **17.** Apertural, **18.** Lateral, **19.** Dorsal, **20.** Apical and **21.** Umbilical views of shell. Petit Collection 2397, Arenas de Quebro, Panama, in 73 m. **22–26.** *Trigonostoma* ("*Extractrix*") *hoerlei* Olsson, 1967. Holotype, USNM 645162, Kissimmee, Florida. **22.** Apertural, **23.** Lateral, **24.** Dorsal, **25.** Apical and **26.** Umbilical views of shell. Scale bar = 3 mm for figure 14; = 1 cm for Figures 15–21; = 1.5 cm for Figures 22–26.

populations expand following a calamity, or when a previously unoccupied or temporarily favorable environment is colonized) (Vermeij, 1987: 42).

Disjunct coiling in *Valvata juliae*, for example, was limited to a short stratigraphic interval within the Pleistocene, and believed to be a response to high levels of environmental stress caused by lake level fluctuations in the Lake Turkana (Scholz and Glaubrecht, 2010).

Rex and Boss (1973) conceded that the selective significance of open coiling is unclear, and recognized that it evolved independently in several unrelated lineages to fill "dissimilar environmental roles." They noted the success of some open-coiled taxa in terms of broad geographic distributions and/or their persistence through geological time. Several lineages with open-coiled shells (e.g., genera within Epitoniidae, Nystiellidae, Architectonicidae) are known to be ectoparasites of cnidarians. Cancellariids are characterized by an alimentary system highly specialized for suctorial feeding on body fluids (Harasewych and Petit, 1998). Depending on species, prey organisms range from sharks and rays (O'Sullivan et al., 1987) to bivalves and gastropods (Loch, 1987).

No cancellariid species have yet been reported to feed on cnidarians. When the habitat and diet of *Extractrix milleri* is better known, it may shed insights on the advantages open coiling bestows on species of the genus *Extractrix*, a lineage that has persisted from the Eocene to the Recent.

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